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RESEARCH ARTICLE

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Individual variation in age-dependent reproduction: Fast explorers live fast but senesce young?

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Abstract

1. Adaptive integration of life history and behaviour is expected to result in variation in the pace-of-life. Previous work focused on whether 'risky' phenotypes live fast but die young, but reported conflicting support. We posit that individuals exhibiting risky phenotypes may alternatively invest heavily in early-life reproduction but consequently suffer greater reproductive senescence.
2. We used a 7-year longitudinal dataset with >1,200 breeding records of >800 female great tits assayed annually for exploratory behaviour to test whether within-individual age dependency of reproduction varied with exploratory behaviour. We controlled for biasing effects of selective (dis)appearance and within-individual behavioural plasticity.
3. Slower and faster explorers produced moderate-sized clutches when young; faster explorers subsequently showed an increase in clutch size that diminished with age (with moderate support for declines when old), whereas slower explorers produced moderate-sized clutches throughout their lives. There was some evidence that the same pattern characterized annual fledgling success, if so, unpredictable environmental effects diluted personality-related differences in this downstream reproductive trait.
4. Support for age-related selective appearance was apparent, but only when failing to appreciate within-individual plasticity in reproduction and behaviour.
5. Our study identifies within-individual age-dependent reproduction, and reproductive senescence, as key components of life-history strategies that vary between individuals differing in risky behaviour. Future research should thus incorporate age-dependent reproduction in pace-of-life studies.

KEYWORDS
age dependence, behaviour, life history, personality, reaction norms, reproduction, senescence, variance partitioning

1 | INTRODUCTION

Life-history theory predicts that organisms resolve trade-offs between current and future reproduction differently depending on ecology (Saether, 1988; Stearns, 1992; Williams, 1966). This may cause variation in life histories along a pace-of-life (POL) slow-to-fast continuum (Ricklefs & Wikelski, 2002). Comparative research demonstrated covariance ('syndrome' structure) between behavioural, physiological and life-history traits among species or populations, called a pace-of-life syndrome (POLS) (Ricklefs & Wikelski, 2002). Current POLS studies address whether among-individual behavioural differences (aka 'personality') co-evolved with POL within populations (Dammhahn, Dingemanse, Niemelä, & Reale, 2018; Réale et al., 2010). Research concentrates on 'risky behaviours' (e.g. aggressiveness, anti-predator boldness, exploration) that facilitate resource acquisition at the cost of reduced life span and may thus function as mediators of life-history trade-offs (Biro & Stamps, 2008, 2010; Careau, Thomas, Humphries, & Réale, 2008; Stamps, 2007; Wolf, Doorn, Leimar, & Weissing, 2007).

Studies of within-population POLSs imply that aggressive, bold or explorative individuals exhibit a 'fast' lifestyle characterized by fast growth, early maturation, increased reproductive output per breeding attempt and a reduced life span. Adaptive theory implies such patterns result from individual variation in residual reproductive value (reviewed by Dingemanse & Wolf, 2010): individuals with low residual reproductive values disproportionally benefit from risky behaviours because they gain reproductive benefits but lose little when such actions reduce life span (Wolf et al., 2007). Support comes from manipulations of early-life conditions, and parental effort, demonstrating that risky behaviour is up- versus down-regulated when residual reproductive value is decreased versus increased (Bateson, Brilot, Gillespie, Monaghan, & Nettle, 2015; Nicolaus et al., 2012). Various studies have already demonstrated that bold individuals 'live fast but die young', confirming POLS-theoretical predictions (reviewed by Réale et al., 2010; Royaute, Berdal, Hickey, & Dochtermann, 2018; Smith & Blumstein, 2008). Other studies, by contrast, report zero or opposite relationships between risky behaviours, reproduction and life span (e.g. Nicolaus, Piault, Ubels, Tinbergen, & Dingemanse, 2016; Niemelä, Dingemanse, Alioravainen, Vainikka, & Kortet, 2013; Santostefano, Wilson, Niemelä, & Dingemanse, 2017); the validity of POLS concept is therefore subject to debate (Mathot & Frankenhuis, 2018; Royaute et al., 2018).

Pace-of-life syndrome studies, however, fail to appreciate that trade-offs between current and future reproduction may, depending on ecology, be resolved in multiple ways (Montiglio, Dammhahn, Messier, & Reale, 2018). That is, POLS research has focussed on survival costs associated with fast life histories (Royaute et al., 2018; Smith & Blumstein, 2008), while the cost of reproduction can also be expressed by an earlier onset of reproductive senescence (Lemaitre et al., 2015). Reproductive senescence is the age-dependent decline in reproductive performance within individuals due to deteriorating physiological and cellular functioning when older, evolved because extrinsic mortality weakens selection with increasing age (Fisher, 1930; Hamilton, 1966; Medawar, 1952; Williams, 1957). Individuals with risky behavioural profiles (as defined above) may thus pay the costs of their fast lifestyle (increased reproductive output per breeding attempt) by reproductively senescing earlier in life. This is in line with laboratory studies showing that bold fish suffer greater oxidative stress and faster telomere attrition (Pauliny, Devlin, Johnsson, & Blomqvist, 2015), while bold fish also have shorter telomeres in the wild (Adriaenssens, Pauliny, Blomqvist, & Johnsson, 2016). The hypothesized integration of reproductive senescence as part of a POLS predicts individuality in age-dependent reproduction within populations, for which ample evidence exists (e.g. Brommer, Rattiste, & Wilson, 2010; Brommer, Wilson, & Gustafsson, 2007; Evans, Gustafsson, & Sheldon, 2011). It further predicts that fast life histories are associated with earlier reproductive senescence, as demonstrated by among-species comparisons (Jones et al., 2008).

By contrast, few studies investigated whether among-individual differences in risky behaviour covary with age-dependent reproduction (Patrick & Weimerskirch, 2015; Réale, Martin, Coltman, Poissant, & Festa-Bianchet, 2009). Importantly, associations between reproduction and age result from two distinct processes (van de Pol & Verhulst, 2006). Reproduction varies with age *within individuals*, first, due to age-related plasticity, and second, due to selective (dis)appearance of low- versus high-quality individuals. For example, individuals producing large clutch sizes throughout their lives ('high-quality' individuals) may also start reproducing when young, or have a long reproductive life. The hypothesized integration of risky behaviour and age-dependent reproduction posits that *within-individual* age-related plasticity varies among behavioural types, requiring approaches that disentangle within- from among-individual age effects (van de Pol & Verhulst, 2006). Similarly, risky behaviours differ among individuals (Bell, Hankison, & Laskowski, 2009; Holtmann, Lagisz, & Nakagawa, 2017) but simultaneously exhibit within-individual age-dependent plasticity (Araya-Ajoy & Dingemanse, 2017; Brommer & Class, 2015; Class & Brommer, 2016; Fisher, David, Tregenza, & Rodriguez-Munoz, 2015; Patrick, Charmantier, & Weimerskirch, 2013). Repeated measures are thus required to estimate relationships between individual-level behaviour and reproductive senescence while avoiding bias due to within-individual plasticity (Niemelä & Dingemanse, 2018a, 2018b). To our knowledge, this is the first study of personality-related age dependency of reproduction that fully applies such approaches.

We tested whether individuals exhibiting risky behavioural profiles also allocated more resources to (early-life) reproduction, and whether they suffered greater reproductive senescence. We used a descriptive approach, acknowledging that experimental studies will be required to test whether personality-related allocation to early-life reproduction represents an investment causally affecting reproduction later in life. We used a longitudinal dataset with 1,209 breeding records of 813 females great tits assayed annually during the reproductive phase for their activity in a small cage (Stuber et al., 2013). Our previous studies demonstrated that activity represents a risky behaviour, implying that it allows for an appropriate test of theory (sensu Carter, Feeney, Marshall, Cowlishaw, & Heinsohn, 2013;

Houle, Pelabon, Wagner, & Hansen, 2011). Active great tits—called 'faster' explorers throughout—behave more boldly when confronted with risk of predation (Stuber et al., 2013) and respond more aggressively to territorial intrusions than 'slower' (less active) explorers (Moiron, Araya-Ajoy, Mathot, Mouchet, & Dingemanse, 2019). In line with POLS predictions, faster great tits also produce larger clutches (Araya-Ajoy et al., 2016) and are more willing to shift investment towards current reproduction when given the opportunity (Nicolaus et al., 2015).

We aimed to estimate within-individual age dependency of annual reproduction, focussing on four reproductive traits determining annual reproductive success: clutch size, nest success (binary probability to produce any fledglings), and for successful nests, fledgling number and average mass. For each trait, we estimated within-individual age dependency of reproduction as a function of exploratory behaviour. Our repeated measures design enabled estimating relationships between individual-level behaviour and reproductive senescence while avoiding bias caused by within-individual plasticity (Niemelä & Dingemanse, 2018a, 2018b).

2 | MATERIALS AND METHODS

2.1 | Field methodology

The study was performed in 12 nest box plots in mixed deciduous forests within a 15 × 20 km^2 area near Munich, Germany (47°58′N, 11°14′E). Each plot consisted of 50 boxes within a regular grid covering ~9 ha. For 7 years (2010–2016), nest boxes were inspected (bi)weekly (April–July) to record lay date (back-calculated assuming one egg laid per day) and clutch size. Shortly before expected hatching, boxes were inspected daily to determine hatch date (day 0). At day 7, each parent was captured with a spring trap inside the box, marked with an aluminium ring and a unique colour ring combination (if not banded previously), and assayed for their activity in a cage (Stuber et al., 2013). This assay represents a version of the classic 'novel environment test' (Dingemanse et al., 2012; Verbeek, Drent, & Wiepkema, 1994) modified for field research (Kluen & Brommer, 2013; Stuber et al., 2013). Briefly, the subject's behaviour was recorded for 2 min with a camera placed 1.5 m in front of the cage (detailed in Stuber et al., 2013). The total number of hops among cage locations was used as a proxy for exploratory behaviour (Araya-Ajoy et al., 2016), where faster explorers had higher scores. Directly following testing, sex and age (first-year breeder vs. older) were determined (based on plumage characteristics; Jenni & Winkler, 1994), standard morphological measurements (body mass, tarsus, bill and wing length) and a blood sample taken, and the bird released (within 15 min post-capture). On day 9, another capture attempt was made if we previously failed to capture both parents. On day 14, mentioned morphological traits were measured for all nestlings alive. Boxes were inspected every second day from day 19 onwards to determine fledgling number. Outside the breeding season, boxes were inspected at night (once or twice per winter), and roosting individuals captured and ringed (Abbey-Lee, Mathot, & Dingemanse, 2016; Mathot, Nicolaus, Araya-Ajoy, Dingemanse, & Kempenaers, 2015; Stuber et al., 2013); the exploration test in the cage was not conducted at this time.

2.2 | Statistical analyses

We first produced a base model estimating population-average within-individual age effects, and the population-average age of peak performance, for key determinants of reproductive success (n = 1,209) of 'first clutches' (clutches initiated within 30 days after the first clutch of the year was found; van Noordwijk, McCleery, & Perrins, 1995). We focused on clutch size, average offspring body mass at day 14 and number of offspring fledged. Visual inspection of raw data and residuals of models (detailed below) showed that traits were sufficiently normally distributed; however, for fledgling number this was only so when excluding first broods failing completely (n = 315 of 1,209 nests; 26%) (Appendix S1). We therefore studied variation in fledgling number by analysing, first, the binary probability to fledge any offspring (n = 1,209 nests), and, second, for successful nests, fledgling number (n = 894 nests). We chose this approach to reduce the number of distributional assumptions, and analytical complexity, associated with alternative (e.g. zero-inflated Poisson) models. Analyses of the binary probability to fledge any offspring implied that total nest failure occurred randomly with respect to key predictors; this was also the case for expanded models (detailed below) where effects of exploratory behaviour were never strongly supported (Appendix S2, Table S2). The subset of nests producing fledglings (n = 894 of 1,209 nests; 74%) thus appeared to represent an unbiased sample; total nest failure is therefore not discussed further. Integrative measures of reproductive fitness, such as the number of offspring recruiting as breeders into the population (Bouwhuis, Sheldon, Verhulst, & Charmantier, 2009), could not be used because our study setup (small nest box plots within larger patches of suitable habitat) resulted in little local recruitment (Nicolaus et al., 2015). As a second step, we constructed an expanded model to determine whether an individual's average level of exploratory behaviour (defined below) predicted its age-dependent reproductive profile. Our previous studies showed that reproductive parameters (like clutch size) are repeatable with respect to female but not male identity (Araya-Ajoy et al., 2016). As our primary interest was in analysing effects of repeatable (i.e. among-individual) differences of exploratory behaviour, we thus focussed on female breeders throughout.

2.2.1 | Defining age categories

We defined age in years since birth, with age = 0 representing the year of birth; great tits breed earliest as 1-year-olds (age = 1). Absolute age was known for any breeder ringed as nestling in our populations ('local recruit'; n = 77 of 813 birds, 9%). The majority of these local recruits bred as 1-year-olds (n = 69 of 77 local recruits, 90%). Absolute age could also be determined for unringed birds identified, based on plumage characteristics, as 1-year-olds (n = 529

of 736 immigrant recruits, 72%). Absolute age could not be determined for immigrants first captured with an adult plumage (implying they were 2-year-olds or older, age ≥ 2; *n* = 207 of 736 immigrant recruits, 28%). Following Bouwhuis et al. (2009), this latter category of immigrants was assumed to have recruited as 2-year-olds. Local recruits not recruiting as 1-year-olds (*n* = 8), all recruited as 2-year-olds, validating this assumption.

2.2.2 | Modelling age effects

Following Bouwhuis et al. (2009), statistical analyses fitted linear and quadratic age to simultaneously model pre-peak improvements and post-peak declines in reproduction. All analyses also fitted 'first observed age' and 'last observed age' of reproduction to control, respectively, for selective appearance and disappearance from the dataset of birds differing in average annual reproductive performance; this avoids biases in estimates of within-individual age effects (van de Pol & Verhulst, 2006). First observed age of reproduction, determined using breeding season and roosting captures (see above), was 1 (*n* = 598 females; 74%), 2 (*n* = 190; 24%), 3 (*n* = 13; 2%), 4 (*n* = 3; <1%) or 5 (*n* = 1; <1%). Fewer than 2% of all females (*n* = 17 of 813 individuals) were (older than) 3 years old at first observed age of reproduction; we therefore pragmatically fitted first observed age as a two-level factor in our analyses (recruited as 1 year old vs. older). Notably, no bird recruiting as a 3 years old or older had breeding records (e.g. second or replacement clutches) from previous years. Rather, those were immigrants previously ringed in our study area (e.g. in winter; see above), that had likely bred previously in natural cavities, whether adjacent to our study area (Drent, 1984) or elsewhere (Harvey, Greenwood, & Perrins, 1979). Last observed age of reproduction was 1 (*n* = 414 females; 51%), 2 (*n* = 237; 29%), 3 (*n* = 101; 12%), 4 (*n* = 44; 5%), 5 (*n* = 12; 1%), 6 (*n* = 4; <1%) or 7 (*n* = 1, <1%). Controlling for differences in last observed age effects between birds with complete life histories (defined as birds not observed for two consecutive years following their last observed productive event; Bouwhuis et al., 2009) versus incomplete life histories (all other birds) did not bias parameters of key interest (Appendix S3 and Table S3a). The same was true when controlling for female body mass (Table S3b). We therefore ignored these variables in analyses reported in the main text.

2.2.3 | Base models

Age effects were modelled by fitting (for each trait separately) a univariate mixed-effect model, where a statistical intercept (β_0), age (β_1), age squared (β_2), first observed age (β_3) and last observed age (β_4) were included as fixed effects (age variables as covariates except for first observed age, see above). Age was fitted as age-1 to ensure that intercepts of our models represented the reproductive performance for the earliest age of first reproduction. Random intercepts were included for individual, plot, year and plot-year identity (unique combination of plot and year); for sample sizes, see Table 1. The latter three random effects controlled, respectively, for unmeasured spatial, temporal and spatiotemporal environmental effects (Araya-Ajoy & Dingemanse, 2017; Araya-Ajoy et al., 2016). We further controlled for brood size manipulations conducted in 2010 and 2011 (detailed in Appendix S4). Previous analyses showed that slower explorers had highest reproductive success when given experimental brood sizes equal to their natural choice, while faster explorers had highest reproductive success when given increased brood sizes (Nicolaus et al., 2015). Neither reproductive traits (e.g. clutch size, fledgling number) nor exploratory behaviour were affected by perceived predation levels (manipulated in 2013 and 2014; see Table S1 in Abbey-Lee & Dingemanse, 2019). Exploratory behaviour also did not vary with observer identity (Moiron et al., 2019). We therefore did not consider these factors further. Models assumed a binomial (probability to produce any fledglings) or Gaussian error distribution (all other traits).

For any reproductive trait with statistical evidence (defined below) for quadratic within-individual age effects, we also estimated (a) the age of peak reproduction as $-\beta_1/2\beta_2$, and (b) the associated reproductive performance at this age ('peak performance') as $\beta_0 - \beta_1^2/4\beta_2$ (Bronshtein, Semendyayev, Musiol, & Mühlig, 2015); the uncertainty associated with these derived parameters was calculated by taking forward the posterior distribution of each fixed-effect parameter. Importantly, quadratic age effects can occur due to pre-peak age-dependent improvements and/or post-peak age-dependent declines (senescence). A priori planned post hoc analyses were performed for any reproductive trait exhibiting quadratic effects to estimate pre- and post-peak age effects (Bouwhuis et al., 2009; Keller, Reid, & Arcese, 2008; Reid, Bignal, Bignal, McCracken, & Monaghan, 2003). This was achieved by replacing the quadratic effect of age from the base model for two new fixed effects: (a) a binary variable 'pre-peak' (coded '0' for post-peak ages and '1' for pre-peak ages) and (b) the interaction between linear age and pre-peak. The main effect of age in this post hoc model represents the post-peak age effect while the interaction estimates the pre-peak age effect as a deviation from the post-peak age effect; the sum of the two represents the pre-peak age effect.

Models fitting parabolic age effects enable the calculation of reproductive peaks, but also force symmetrical pre- versus post-peak effects. If pre- and post-peak effects are not symmetrical, estimates of reproductive peaks may become biased. Fortunately, for the two traits showing nonlinear age effects (clutch size and fledging number in non-failed broods), pre- versus post-peak effects of age (which our *post hoc* model, detailed above, estimated independently) were relatively symmetrical (see Results and Table 1). Moreover, a version of Table 1 including the third-order effect of age showed that this effect was supported neither for clutch size (mean ± 95% credible interval (CI): 0.00, −0.03 to 0.02) nor for fledging number (0.03, −0.02 to 0.09). This implies that parabolic models seemed appropriate. We further tested whether the single age category with <5 data points (age = 7; see Results) biased our estimates (see Nussey, Kruuk, Donald, Fowlie, & Clutton-Brock, 2006 for a similar approach). We thus re-ran our main analyses (Table 1) after combining ages 6 and 7, which did not change our estimates (Appendix S5 and Table S5).

TABLE 1 Sources of variation in clutch size, number and average mass of fledglings (for nests producing any fledglings), and exploratory behaviour

	Clutch size	No. of fledglings	Fledgling mass	Exploratory behaviour
	Count	Count	Grams	Count (No. of hops)
Fixed effects	**β (95% CI)**	**β (95% CI)**	**β (95% CI)**	**β (95% CI)**
Intercept[a]	8.14 (7.8, 8.48)	5.36 (4.66, 6.04)	15.13 (14.5, 15.76)	70.11 (66.6, 73.64)
Linear age	0.35 (0.17, 0.54)	0.41 (0.07, 0.77)	0.06 (−0.23, 0.37)	−3.89 (−7.05, −0.79)
Quadratic age	−0.08 (−0.13, −0.03)	−0.14 (−0.24, −0.05)	−0.01 (−0.08, 0.07)	−0.05 (−0.85, 0.76)
First age	−0.13 (−0.39, 0.14)	−0.01 (−0.34, 0.32)	0.2 (−0.1, 0.52)	5.53 (1.98, 9.16)
Last age	−0.02 (−0.14, 0.09)	0.04 (−0.1, 0.18)	0 (−0.13, 0.13)	−0.04 (−1.52, 1.52)
BSM: control (0)	NA	0.13 (−0.49, 0.78)	−0.38 (−0.95, 0.17)	2.36 (−3.61, 8.35)
BSM: enlarged (+3)	NA	1.44 (0.79, 2.06)	−0.59 (−1.12, −0.07)	−1.77 (−7.31, 3.83)
BSM: reduced (−3)	NA	−1.34 (−1.96, −0.73)	−0.48 (−1.01, 0.03)	0.88 (−4.75, 6.78)
Random effects	**σ^2 (95% CI)**	**σ^2 (95% CI)**	**σ^2 (95% CI)**	**σ^2 (95% CI)**
Individual	1.48 (1.36, 1.61)	0.22 (0.19, 0.26)	0.43 (0.37, 0.49)	143.75 (129.3, 159.83)
Plot × Year	0.04 (0.03, 0.05)	0.26 (0.19, 0.35)	0.33 (0.24, 0.43)	0.78 (0.55, 1.04)
Plot	0.07 (0.03, 0.12)	0.24 (0.09, 0.46)	0.21 (0.09, 0.39)	13.53 (5.2, 25.58)
Year	0.14 (0.08, 0.24)	0.77 (0.34, 1.46)	0.59 (0.27, 1.09)	11.29 (4.14, 23.38)
Residual	0.83 (0.76, 0.9)	3.02 (2.75, 3.31)	2.23 (2.04, 2.44)	275.99 (253.82, 298.84)
Adjusted Repeatability	**r (95% CI)**	**r (95% CI)**	**r (95% CI)**	**r (95% CI)**
Individual	0.58 (0.55, 0.61)	0.05 (0.04, 0.06)	0.11 (0.1, 0.13)	0.32 (0.3, 0.35)
Plot × Year	0.02 (0.01, 0.02)	0.06 (0.04, 0.08)	0.09 (0.06, 0.11)	0 (0, 0)
Plot	0.03 (0.01, 0.05)	0.05 (0.02, 0.1)	0.06 (0.02, 0.1)	0.03 (0.01, 0.06)
Year	0.06 (0.03, 0.09)	0.17 (0.08, 0.28)	0.15 (0.08, 0.26)	0.03 (0.01, 0.05)
Residual	0.32 (0.3, 0.35)	0.67 (0.58, 0.75)	0.59 (0.52, 0.65)	0.62 (0.59, 0.65)
Peak performance	**β (95% CI)**	**β (95% CI)**	**β (95% CI)**	**β (95% CI)**
Trait value at peak[b]	8.56 (8.14, 8.98)	5.67 (4.9, 6.44)	NA	NA
Age at peak[c]	3.4 (2.66, 4.68)	2.4 (1.5, 3.16)	NA	NA
Pre-/post-peak analysis	**β (95% CI)**	**β (95% CI)**	**β (95% CI)**	**β (95% CI)**
Pre-peak age effect[d]	0.2 (0.08, 0.32)	0.36 (0.01, 0.72)	NA	NA
Post-peak age effect[e]	−0.24 (−0.6, 0.13)	−0.51 (−0.89, −0.12)	NA	NA
Sample sizes	**n**	**n**	**n**	**n**
Plot Year	84	84	84	84
Plot	12	12	12	12
Year	7	7	7	7
Individual	813	625	671	791
Observations	1,209	894	962	1,154

Note: We provide fixed-effect parameter estimates (β) with 95% credible intervals (CIs) for linear (age) and quadratic (age × age) effects of absolute age (years) within-individual females for a model controlling for effects of selective (dis)appearance by fitting first and last observed age. Birds breeding in their second year of life (i.e. 1-year-olds) were given age equal to zero such that the intercept value was for this category of bird. BSM stands for brood size manipulations performed in 2010 and 2011. Individual, plot year, plot and year were fitted as random effects; variance attributable to each effect is printed both as an absolute value (σ^2) and as a proportion of the variance not attributable to random effects (adjusted repeatability, r) with 95% credible intervals (CIs). For traits exhibiting nonlinear age effects, we further provide the estimated (i) trait value and (ii) age at peak performance, as well as the effect of age (iii) pre- and (iv) post-peak.

[a]Estimate is for 1-year-old birds (reference group; age−1 = 0); for all traits except clutch size, brood size manipulation category was fitted as an additional fixed-effect factor with 'not manipulated' set as the reference category (see Appendix S4). The statistical intercept is therefore for 1-year-old birds that were not manipulated.

[b]Calculated as $\beta_0 - \beta_1^2/4\beta_2$, where β_0 = the statistical intercept, β_1 = age−1 (linear term), β_2 = age−1 (quadratic term); not calculated for traits failing to exhibit significant quadratic age effects ('NA').

[c]Calculated as $-\beta_1/2\beta_2$, where β_1 = age-1 (linear term), β_2 = age−1 (quadratic term); we added the value one (i.e. to back-transform age), such that age = 0 again reflected the age of birth; not calculated for traits failing to exhibit significant quadratic age effects ('NA').

[d]Effect of linear age before peak performance (post hoc analysis; detailed in the Methods).

[e]Effect of linear age after peak performance (post hoc analysis; detailed in the Methods).

2.2.4 | Expanded models: estimating effects of individual-level exploratory behaviour

We expanded our base models to test whether within-individual age effects on reproduction varied with an individual's average value for exploratory behaviour (defined below). We did so by first estimating sources of variation in exploratory behaviour by fitting a univariate mixed-effects model with a fixed and random effects structure as detailed above (Table 1), after which we simulated (using the R-package *arm*, see below) each individual's best linear unbiased predictor (BLUP) 1,000 times, and defined an individual's average value for exploratory behaviour as its mean BLUP over all simulations (i.e. producing one BLUP per individual). From previous work, we know that great tits habituate when repeatedly subjected to the novel environment test; in this and other (Dingemanse et al., 2012), great tit datasets, age and inter-year test sequence are fully conflated by design (i.e. surviving birds are subjected to repeated tests when older). Pragmatically fitting age (though functionally hard to interpret) thus enabled us to avoid bias in our estimates of individual-specific average values. Next, we expanded our base models by including each individual's average level (BLUP) of exploratory behaviour as a mean and variance-standardized covariate; we then fitted its interaction with each of the four age variables (i.e. age, age squared, first and last observed age) (Table 2). The usage of BLUPs as covariates has been criticized when uncertainty associated with BLUPs is not taken forward (Hadfield, Wilson, Garant, Sheldon, & Kruuk, 2010; Houslay & Wilson, 2017). Appendix S6 describes simulations demonstrating that taking forward uncertainty in BLUP values resulted in biased estimates; fitting average BLUP values instead produced estimates that were less precise yet unbiased; average BLUP values were therefore used throughout.

2.2.5 | Model implementation

Statistical analyses were carried out using the packages 'LME4' and 'ARM' in R-v3.3.2 (R Development Core Team, 2017). Model fit was assessed by visual inspection of the residuals (see Appendix S1). Based on 5,000 simulations, we extracted the 95% CIs (Gelman & Hill, 2007), representing the uncertainty around our estimates. Assessment of statistical support was thus obtained from the posterior distribution of each parameter, simulated using the *sim* function. We considered an effect 'strongly supported' if zero was not included within the 95% CI, and 'moderately supported' if the point estimate was skewed away from zero while its 95% CI simultaneously overlapped zero. Estimates centred on zero were viewed as strong support for the absence of an effect.

3 | RESULTS

We acquired reproductive data for 599 (age = 1; 49.5% of all broods), 379 (age = 2; 31.3%), 151 (age = 3; 12.5%), 58 (age = 4; 4.8%), 16 (age = 5; 1.3%), 5 (age = 6; 0.4%) and 1 (age = 7; 0.1%) annual first clutches. For 95% (1,154 of 1,209), we assayed female exploratory behaviour, which we subsequently used to calculate a single average value (see Methods) for each individual over all its assays; average exploratory behaviour was therefore available for 98% (1,187) of all clutches.

3.1 | Exploratory behaviour

Exploratory behaviour dropped from 70.11 hops per (2-min) assay in 1-year-olds (intercept value; Table 1) with 3.89 hops per assay per year of age (negative effect of linear age; Table 1; Figure 1a); nonlinear age effects were not supported (quadratic age effect; Table 1). A first observed age effect was strongly supported (Table 1). Specifically, females first breeding when 2 years old or older (age ≥ 2) were behaving faster than birds recruiting as 1-year-olds (Figure 1a). Females were moderately repeatable in behaviour across years: adjusted individual cross-year repeatability (r) was 0.32 (Table 1). Plot, year and plot-year identity explained little variation if any at all (Table 1).

3.2 | Clutch size

Clutch size varied within the average female as a function of linear and quadratic age (Table 1; Figure 1b). Clutch size was highest for 3-year-olds (age at peak: 3.4; Table 1). Before the age of peak performance, clutch size increased with 0.20 eggs per year of age (pre-peak age effect). Afterwards, clutch size decreased with 0.24 eggs per year (post-peak age effect); this decrease was moderately supported (Table 1). Clutch size thus showed age-dependent improvements that diminished with age, likely followed by a post-peak decline due to reproductive senescence.

Female exploratory behaviour predicted how clutch size varied with age. The main effect of exploratory behaviour centred on zero (Table 2); because we left-centred age (see Methods), this implied that exploratory behaviour did not affect clutch size among 1-year-olds. Instead, exploratory behaviour affected subsequent changes with age: exploratory behaviour interacted with both linear (moderate support) and quadratic (strong support) age (Table 2). Plots of parameter estimates for linear (Figure 2a) and quadratic (Figure 2b) age effects as a function of exploratory behaviour visualized the statistical nature of these interactions. These plots implied that the slowest half of females (values < 0) did not change clutch size with age: their parameter estimates for linear (Figure 2a) and quadratic (Figure 2b) age centred on zero. Consequently, the 50% slowest explorers produced moderate-sized clutches throughout their reproductive lives (Figure 3a, raw data controlling for random effects; Figure 3c, model predictions). By contrast, there was strong support for the fastest half (values ≥ 0) to exhibit age-dependent clutch sizes: credible intervals for this group did not overlap zero for either linear (Figure 2a) or quadratic (Figure 2b) age effects. These 50% fastest explorers improved clutch size with age in a diminishing fashion, possibly followed by an age-dependent decline (i.e. reproductive senescence) when old (Figure 3b, raw data controlling for random effects; Figure 3d, model predictions). We came to the

TABLE 2 Effects of individual exploratory behaviour on within-individual age dependency of reproductive traits: clutch size, and number and average mass of fledglings (for nests producing any fledglings)

	Clutch size	No. of fledglings	Fledgling mass
	Count	Count	Grams
Fixed effects	**β (95% CI)**	**β (95% CI)**	**β (95% CI)**
Intercept	8.15 (7.82, 8.49)	5.34 (4.62, 6.05)	15.14 (14.52, 15.75)
Linear age	0.31 (0.12, 0.49)	0.37 (−0.01, 0.74)	0.1 (−0.21, 0.42)
Quadratic age	−0.06 (−0.11, −0.01)	−0.12 (−0.22, −0.02)	−0.02 (−0.1, 0.06)
First age	−0.11 (−0.38, 0.17)	0 (−0.36, 0.35)	0.17 (−0.13, 0.48)
Last age	−0.03 (−0.14, 0.09)	0.04 (−0.11, 0.18)	−0.01 (−0.13, 0.12)
BSM: control (0)	NA	0.27 (−0.39, 0.93)	−0.35 (−0.91, 0.22)
BSM: enlarged (+3)	NA	1.49 (0.83, 2.14)	−0.54 (−1.1, 0.01)
BSM: reduced (−3)	NA	−1.28 (−1.92, −0.63)	−0.43 (−0.98, 0.1)
Exploration	−0.04 (−0.2, 0.12)	0.08 (−0.13, 0.31)	0.01 (−0.18, 0.2)
Exploration × Linear age	0.15 (0, 0.3)	0.05 (−0.24, 0.37)	−0.08 (−0.35, 0.18)
Exploration × Quadratic age	−0.05 (−0.09, −0.01)	−0.04 (−0.11, 0.04)	0.02 (−0.05, 0.09)
Exploration × First age	−0.41 (−0.69, −0.14)	0 (−0.33, 0.32)	0.26 (−0.03, 0.57)
Exploration × Last age	0.08 (−0.01, 0.18)	0.01 (−0.11, 0.13)	0.02 (−0.09, 0.13)
Random effects	**σ^2 (95% CI)**	**σ^2 (95% CI)**	**σ^2 (95% CI)**
Individual	1.49 (1.37, 1.62)	0.23 (0.2, 0.26)	0.4 (0.35, 0.46)
Plot × Year	0.04 (0.03, 0.05)	0.26 (0.19, 0.35)	0.34 (0.25, 0.45)
Plot	0.07 (0.03, 0.12)	0.26 (0.1, 0.51)	0.19 (0.08, 0.37)
Year	0.14 (0.08, 0.24)	0.77 (0.35, 1.58)	0.53 (0.27, 1.03)
Residual	0.82 (0.76, 0.89)	3.01 (2.74, 3.32)	2.27 (2.07, 2.49)
Adjusted repeatability	***r* (95% CI)**	***r* (95% CI)**	***r* (95% CI)**
Individual	0.58 (0.55, 0.61)	0.05 (0.04, 0.06)	0.11 (0.09, 0.12)
Plot × Year	0.02 (0.01, 0.02)	0.06 (0.04, 0.08)	0.09 (0.07, 0.12)
Plot	0.03 (0.01, 0.05)	0.06 (0.02, 0.11)	0.05 (0.02, 0.09)
Year	0.05 (0.03, 0.09)	0.17 (0.09, 0.3)	0.14 (0.08, 0.24)
Residual	0.32 (0.3, 0.34)	0.66 (0.56, 0.74)	0.61 (0.53, 0.66)
Sample sizes	***n***	***n***	***n***
Plot Year	84	84	84
Plot	12	12	12
Year	7	7	7
Individual	791	610	655
Observations	1,187	879	946

Note: Fixed and random parameters are detailed in Table 1. We print here our expanded models that include an individual's estimated average exploratory behaviour ('Exploration', representing the individual's best linear unbiased predictor derived from the analysis printed in Table 1), and its interactions with all age variables, as additional fixed effects.

same conclusion when we re-ran our models with the same random and fixed-effect structure as printed in Table 1 but separately for each of the two groups. In the slowest half, neither linear (parameter estimate with 95% CIs: −0.06, −0.35 to 0.23) nor quadratic (0.04, −0.05 to 0.12) effects of age were supported (Figure 3c); by contrast, in the fastest half of the females, linear (0.62, 0.37–0.85) and quadratic (−0.13, −0.18 to −0.07) effects of age were both supported (Figure 3d).

Importantly, the distribution of ages differed between the 50% slowest versus fastest explorers. The slowest explorers only had reproductive data for 1- to 5-year-olds (ages 1–5: n = 293, 187, 73, 28, 8 first clutches), the fastest explorers instead for 1- to 7-year-olds (ages 1–7: n = 295, 182, 77, 30, 8, 5, 1). A follow-up analysis using only ages where both had data (i.e. excluding n = 6 data points of age > 5) resulted in the same level of support for interactive effects between exploratory behaviour and linear and quadratic age (Table S7). Thus,

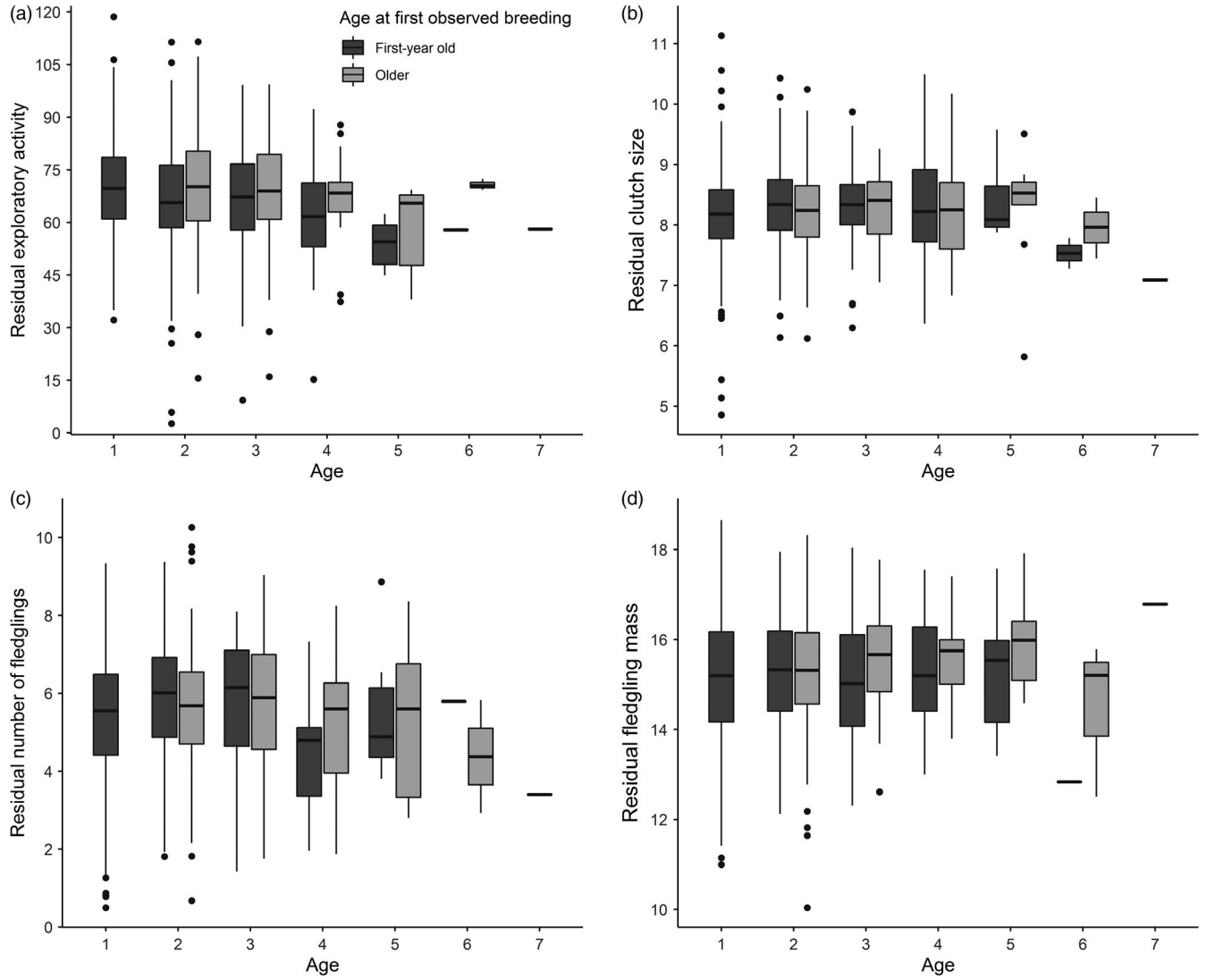

FIGURE 1 Box plots per age class for (a) exploratory behaviour, (b) clutch size, (c) number of fledglings (for non-failed nests) and (d) average fledgling mass. Plotted are residuals from a model controlling solely for random effects listed in Table 1. Separate box plots for birds with first observed age equal to one year old versus older

our finding of personality-related age dependency of clutch size was not an artefact caused by lack of data for older slow explorers.

Note that those post hoc analyses of discrete groups (slower vs. faster explorers) enabled us to interpret, and verbally present, complex interaction terms between continuous predictors (age and exploratory behaviour), and should not be taken as evidence for the existence of two discrete forms of age-dependent clutch sizes within the population.

3.3 | Annual fledgling number and average mass

Annual fledgling number (in non-failing broods) varied within individuals with both linear and quadratic age (Table 1; Figure 1b). Peak performance occurred when birds were between 2 and 3 years old (Table 1). Before the age of peak performance, fledgling number increased with 0.36 offspring per year of age (pre-peak age effects; Table 1). Afterwards, it decreased with 0.51 offspring per year of age (post-peak age effects; Table 1). Annual fledging number showed age-dependent improvements with increased breeding experience (pre-peak age effect), followed by an age-dependent decline due to reproductive senescence (post-peak age effect) that was strongly supported.

Point estimates for interactions between linear (or quadratic) age and exploratory behaviour suggested that the same pattern of personality-related age-dependent reproduction described above for clutch size also characterized fledging number (Table 2). For fledgling number, however, the support was moderate at best owing to skewed 95% CIs (particularly for exploratory behaviour × quadratic age) that nevertheless included zero.

Average fledging mass did not vary with linear or quadratic age (Table 1; Figure 1d), neither did those effects vary as a function of female exploratory behaviour (Table 2).

3.4 | Selective (dis)appearance

We detected no evidence for selective (dis)appearance effects: first and last observed age of reproduction effects were not supported (Table 1).

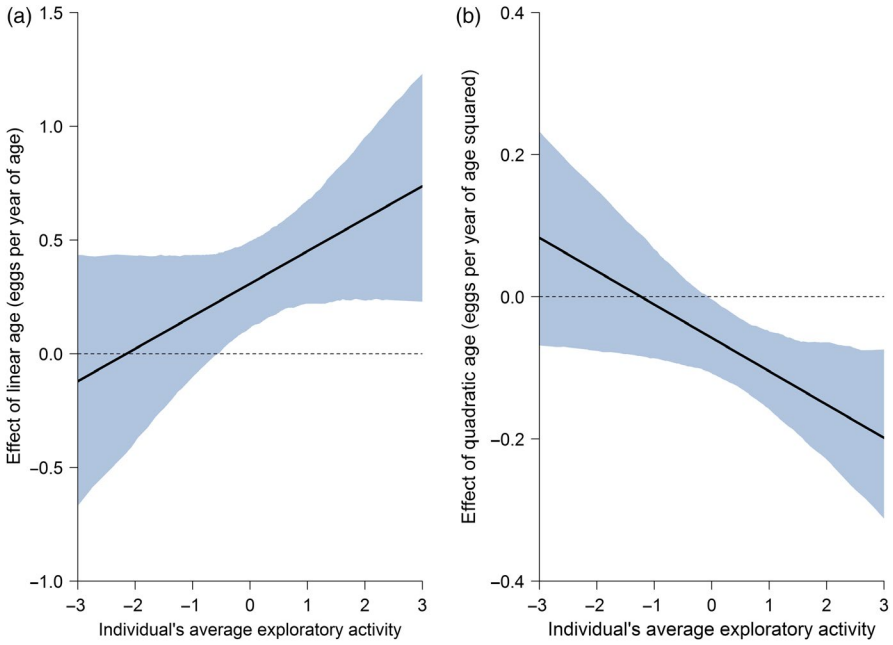

FIGURE 2 The within-individual effect of (a) linear and (b) quadratic age on clutch size (eggs per year of age) as a function of an individual's average exploratory behaviour. The black line represents the point estimate with 95% credible intervals (CIs; blue shaded area) derived from the analysis printed in Table 2. Linear and quadratic age effects were supported only for the 50% fastest explorers (values ≥ 0) and were, respectively, positive versus negative

Our expanded analyses showed that first observed age effects were not supported for birds of average exploratory behaviour (main effect of first observed age; Table 2), echoing results of our main analyses (Table 1). However, there was strong support for a first observed age effect to decrease with increasing exploratory behaviour (interaction first observed age × exploratory behaviour; Table 2). Inspection of the raw data suggested this interaction resulted from faster—but not slower—explorers exhibiting decreased clutch sizes when they were older than first-year-olds at first observed breeding (Figure 3a,b).

4 | DISCUSSION

Optimal behavioural phenotypes should vary with how life-history trade-offs are resolved (Réale et al., 2010; Ricklefs & Wikelski, 2002; Wolf et al., 2007). Adaptive theory predicts that aggressive, bold or explorative individuals trade-off future for current reproduction, leading to a faster pace-of-life (Dammhahn et al., 2018; Mathot & Frankenhuis, 2018; Réale et al., 2010). Previous tests utilizing life span as a proxy for allocation to future reproduction failed to overall support pace-of-life syndrome (POLS) theory (meta-analyses: Royaute et al., 2018; Tarka, Guenther, Niemelä, Nakagawa, & Noble, 2018). We identified here within-individual patterns of age-dependent reproduction, and potentially reproductive senescence, as key components of life history varying with individual risky behaviour. Specifically, slower explorers produced moderate-sized clutches throughout their reproductive lives, showing neither evidence for age-related improvements when young nor evidence for age-related declines when older (Figure 3a,c), though we note that data for old age classes were not available for slower explorers. By contrast, over the same range of age classes as observed for slower explorers (1- to 4-year-olds), faster explorers instead showed age-related improvements that diminished with age (Figure 3b,d). There was moderate support for faster explorers subsequently showing reproductive senescence, though this evidence should be taken with caution as it is based on little data. Importantly, the same pattern may have characterized annual fledgling success, if so, unpredictable environmental effects diluted personality-related differences in this downstream reproductive trait (see also Hutfluss & Dingemanse, 2019 for a similar finding and further discussion). Overall, future studies should consider reproductive senescence as a key component of life history mediating personality-related differences in how trade-offs between current and future reproduction are resolved.

First-year-olds produced moderate-sized clutches regardless of exploration type. Faster explorers subsequently showed age-related increases in clutch size that lasted until they were 3-year-olds (Figure 3b). The majority of breeding records (93.3%) were for birds breeding as 1-year (49.5%), 2-year (31.3%) or 3-year (12.5%)-olds, implying that faster explorers produced, on average, larger clutches than slower explorers for most of their reproductive lives; very few faster explorers thus lived long enough to experience reproductive declines at old age. Importantly, faster explorers cannot be shown to not have a shorter life span in this (Wischhoff & Dingemanse, In Preparation) or other great tit populations (Nicolaus et al., 2016). Slower explorers thus differed from faster ones in two important ways. First, only faster explorers showed (nonlinear) age-related increases in clutch size, likely followed by reproductive senescence. Second, faster explorers produced larger clutches for most of their reproductive life compared to slower explorers. If these age-related increases in clutch size observed in faster explorers represented an investment trading off with future reproduction, an assumption warranting experimental confirmation (Nicolaus et al., 2015), the moderately supported evidence for reproductive senescence among faster explorers may imply that they paid the costs of reproduction by

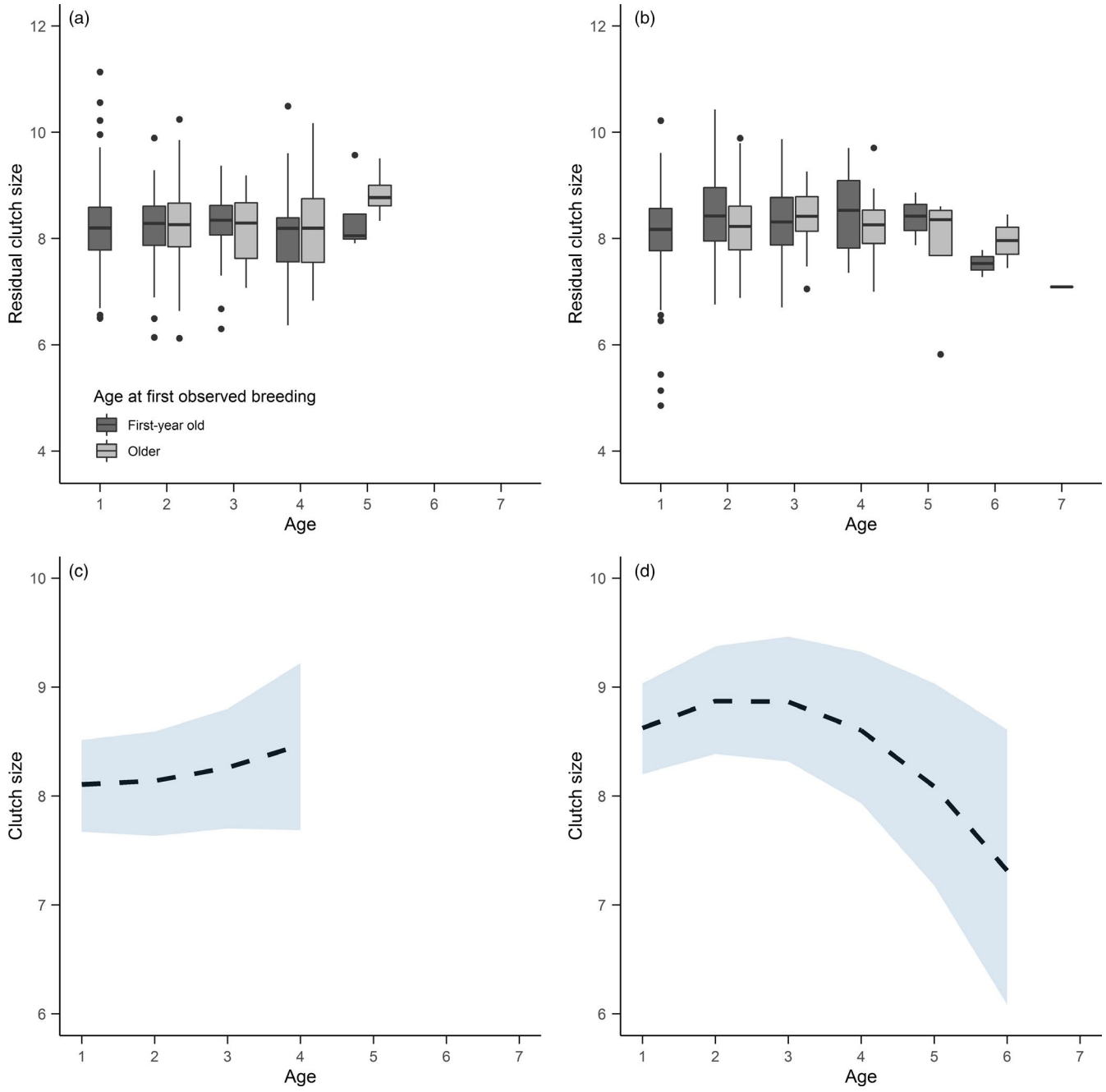

FIGURE 3 Personality-related age dependency of clutch size. We show box plots per age class for the 50% (a) slowest versus (b) fastest explorers; we plot residuals from a model controlling for random effects listed in Table 1, with separate box plots for first observed age equal to one year old versus older. We also plotted the average pattern of within-individual age dependency of clutch size within the (c) 50% slowest versus (d) fastest explorers; the black line represents the point estimate with 95% credible intervals (CIs; blue shaded area) derived from the analysis printed in Table 2

reducing investment in physiological and cellular functioning in late life (see Introduction). Importantly, a recent simulation study implied that POLS-related variation in life-history traits measured once (e.g. longevity) will be extremely difficult to demonstrate empirically compared to POLS-related variation in life-history traits expressed repeatedly (e.g. clutch size) (Araya-Ajoy et al., 2018). We therefore need to be somewhat cautious in interpreting publications failing to recover patterns of reduced longevity among faster explorers from empirical data.

4.1 | Selective (dis)appearance and variation in experience

In this paper, we estimated within-individual patterns of age-dependent reproduction while controlling for potential biases resulting from within-individual behavioural plasticity and selective (dis)appearance of high- versus low-quality individuals. Females were moderately repeatable in reproductive traits; individuals of superior 'quality' (defined statistically as females with high intercepts for reproductive

traits) might thus, for example, have recruited into the breeding population younger ('selective appearance'; first observed age effect), and/or disappeared when older ('selective disappearance'; last observed age effect) (Bouwhuis et al., 2009). For a conceptual illustration of the idea, see Figure 1 in van de Pol and Verhulst (2006).

A first observed age effect explained variation in exploratory behaviour (Table 1; Figure 1a). Specifically, females first breeding as 1-year-olds were slower than females first breeding at older ages (Figure 1a). We offer two potential explanations. First, faster (vs. slower) explorers might recruit into the breeding population at an older age (selective appearance); this might explain why 'late' recruits produced, on average, 5.53 more hops (Table 1). Alternatively, late recruits might have hopped more because they lacked at least 1 year of experience with the assay. This latter explanation seemed more fitting because exploratory behaviour *decreased* with 3.89 hops per year of age (=experience; see Methods) *within* individual females, implying that 'late' recruits (lacking 1 year of experience) should hop more. Indeed, the effect of first observed age was not supported when this differential experience was statistically accounted for (Appendix S8).

Along the same lines, our analyses strongly supported an interactive effect of first observed age and exploratory behaviour on clutch size. This pattern did not imply personality-related selective appearance in the breeding population. Briefly, we observed age-related increases in clutch size solely for faster explorers (Figure 3b,d). A negative interaction between first observed age and exploratory behaviour on clutch size should thus emerge if such effects were attributable to breeding experience rather than age per se: 'late' recruiting faster explorers should lack breeding experience and thus produce smaller clutches. The interactive effect of first observed age and exploratory behaviour on clutch size thus does not constitute sound evidence for personality-related selective appearance; rather, it was expected because breeding experience (i.e. plasticity) affects reproductive performance.

In summary, while we did not find convincing evidence for selective (dis)appearance, we did learn that controlling for first observed age of reproduction provided a means to statistically control for individual differences in age-related experience. For example, it enabled us to conclude that the smaller clutch sizes produced by faster explorers recruiting at an older age were expected based on increases in clutch size with breeding experience. Moreover, exploratory behaviour varied with age and/or experience within individuals, implying that our concerns regarding effects of within-individual plasticity biasing estimates of personality-related age-dependent reproduction (see Introduction) were valid. Future studies should thus carefully consider multiple alternative explanations when interpreting age-related patterns in reproduction.

5 | CONCLUSIONS

We demonstrated for a natural bird population that slower and faster explorers produced moderate-sized clutch sizes when young, after which faster explorers increased nonlinearly, peaked and likely decreased their clutch sizes while ageing, while slower explorers produced moderate-sized clutches throughout. Age-related reproduction thus represents a key component of POLSs. Certain parameters, particularly estimates of the age of peak reproduction or post-peak declines in reproductive performance, were, notably, based on relatively few data, particularly among older age classes. Those estimates are therefore relatively uncertain and warrant validation with larger samples. Experimental studies are further required to reveal whether trade-offs indeed underpin the covariance between life-history traits and risky personality identified in this paper.

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AUTHORS' CONTRIBUTIONS

The study was conceived by N.J.D., and developed and operationalized with input from all authors. Analytical strategies designed and statistical analyses were performed by N.J.D., with input from M.M., and Y.G.A-A, and A.M. A.M. also coordinated the fieldwork and managed the database; all authors contributed to data collection. N.J.D. drafted the manuscript with input from all authors.

DATA AVAILABILITY STATEMENT

Data used in this work are available from Dryad Digital Repository: https://doi.org/10.5061/dryad.12jm63xss (Dingemanse, Moirón, Araya-Ajoy, Mouchet, & Abbey-Lee, 2019).

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REFERENCES

Abbey-Lee, R. N., & Dingemanse, N. J. (2019). Adaptive individual variation in phenological responses to perceived predation

levels. *Nature Communications*, *10*, 1601. https://doi.org/10.1038/s41467-019-09138-5

Abbey-Lee, R., Mathot, K. J., & Dingemanse, N. J. (2016). Behavioral and morphological responses to perceived predation risk: A field experiment in passerines. *Behavioral Ecology*, *27*, 857–864. https://doi.org/10.1093/beheco/arv228

Adriaenssens, B., Pauliny, A., Blomqvist, D., & Johnsson, J. I. (2016). Telomere length covaries with personality in wild brown trout. *Physiology and Behavior*, *165*, 217–222. https://doi.org/10.1016/j.physbeh.2016.07.005

Araya-Ajoy, Y. G., Bolstad, G. H., Brommer, J., Careau, V., Dingemanse, N. J., & Wright, J.. (2018) Demographic measures of an individual's "pace of life": fecundity rate, lifespan, generation time, or a composite variable? *Behavioral Ecology and Sociobiology*, *72*(5), 75. https://doi.org/10.1007/s00265-018-2477-7

Araya-Ajoy, Y. G., & Dingemanse, N. J. (2017). Repeatability, heritability, and age-dependence of seasonal plasticity in aggressiveness in a wild passerine bird. *Journal of Animal Ecology*, *86*, 227–238. https://doi.org/10.1111/1365-2656.12621

Araya-Ajoy, Y. G., Kuhn, S., Mathot, K. J., Mouchet, A., Mutzel, A., Nicolaus, M., … Dingemanse, N. J. (2016). Sources of (co)variation in alternative siring routes available to male great tits (*Parus major*). *Evolution*, *70*, 2308–2321.

Bateson, M., Brilot, B. O., Gillespie, R., Monaghan, P., & Nettle, D. (2015). Developmental telomere attrition predicts impulsive decision-making in adult starlings. *Proceedings of the Royal Society B: Biological Sciences*, *282*, 20142140. https://doi.org/10.1098/rspb.2014.2140

Bell, A. M., Hankison, S. J., & Laskowski, K. L. (2009). The repeatability of behaviour: A meta-analysis. *Animal Behaviour*, *77*, 771–783. https://doi.org/10.1016/j.anbehav.2008.12.022

Biro, P. A., & Stamps, J. A. (2008). Are animal personality traits linked to life-history productivity? *Trends in Ecology and Evolution*, *23*, 361–368. https://doi.org/10.1016/j.tree.2008.04.003

Biro, P. A., & Stamps, J. A. (2010). Do consistent individual differences in metabolic rate promote consistent individual differences in behavior? *Trends in Ecology and Evolution*, *25*, 653–659. https://doi.org/10.1016/j.tree.2010.08.003

Bouwhuis, S., Sheldon, B. C., Verhulst, S., & Charmantier, A. (2009). Great tits growing old: Selective disappearance and the partitioning of senescence to stages within the breeding cycle. *Proceedings of the Royal Society B-Biological Sciences*, *276*, 2769–2777. https://doi.org/10.1098/rspb.2009.0457

Brommer, J. E., & Class, B. (2015). The importance of genotype-by-age interactions for the development of repeatable behavior and correlated behaviors over lifetime. *Frontiers in Zoology*, *12*, S2. https://doi.org/10.1186/1742-9994-12-S1-S2

Brommer, J., Rattiste, K., & Wilson, A. (2010). The rate of ageing in a long-lived bird is not heritable. *Heredity*, *104*, 363–370. https://doi.org/10.1038/hdy.2009.125

Brommer, J. E., Wilson, A. J., & Gustafsson, L. (2007). Exploring the genetics of aging in a wild passerine bird. *The American Naturalist*, *170*, 643–650. https://doi.org/10.1086/521241

Bronshtein, I. N., Semendyayev, K. A., Musiol, G., & Mühlig, H. (2015). *Handbook of mathematics*. Berlin, Heidelberg: Springer-Verlag.

Careau, V., Thomas, D., Humphries, M. M., & Réale, D. (2008). Energy metabolism and animal personality. *Oikos*, *117*, 641–653. https://doi.org/10.1111/j.0030-1299.2008.16513.x

Carter, A. J., Feeney, W. E., Marshall, H. H., Cowlishaw, G., & Heinsohn, R. (2013). Animal personality: What are behavioural ecologists measuring? *Biological Reviews*, *88*, 465–475. https://doi.org/10.1111/brv.12007

Class, B., & Brommer, J. E. (2016). Senescence of personality in a wild bird. *Behavioral Ecology and Sociobiology*, *70*, 733–744. https://doi.org/10.1007/s00265-016-2096-0

Dammhahn, M., Dingemanse, N. J., Niemelä, P. T., & Reale, D. (2018). Pace-of-life syndromes: a framework for the adaptive integration of personality and life-history. *Behavioral Ecology and Sociobiology*, *72*, 62.

Dingemanse, N. J., Bouwman, K. M., van de Pol, M., van Overveld, T., Patrick, S. C., Matthysen, E., & Quinn, J. L. (2012). Variation in personality and behavioural plasticity across four populations of the great tit *Parus major*. *Journal of Animal Ecology*, *81*, 116–126. https://doi.org/10.1111/j.1365-2656.2011.01877.x

Dingemanse, N. J., Moirón, M., Araya-Ajoy, Y. G., Mouchet, A., & Abbey-Lee, R. N. (2019). Data from: Individual variation in age-dependent reproduction: Fast explorers live fast but senesce young? *Dryad Digital Repository*, https://doi.org/10.5061/dryad.12jm63xss

Dingemanse, N. J., & Wolf, M. (2010). A review of recent models for adaptive personality differences. *Philosophical Transactions of the Royal Society B-Biological Sciences*, *365*, 3947–3958.

Drent, P. J. (1984). Mortality and dispersal in summer and its consequences for the density of great tits *Parus major* at the onset of autumn. *Ardea*, *72*, 127–162.

Evans, S. R., Gustafsson, L., & Sheldon, B. C. (2011). Divergent patterns of age-dependence in ornamental and reproductive traits in the collared flycatcher. *Evolution*, *65*, 1623–1636. https://doi.org/10.1111/j.1558-5646.2011.01253.x

Fisher, D. N., David, M., Tregenza, T., & Rodriguez-Munoz, R. (2015). Dynamics of among-individual behavioral variation over adult lifespan in a wild insect. *Behavioral Ecology*, *26*, 975–985. https://doi.org/10.1093/beheco/arv048

Fisher, R. A. (1930). *The genetical theory of natural selection*. Oxford, UK: Oxford University Press.

Gelman, A., & Hill, J. (2007). *Data analysis using regression and multi-variate/hierarchical models*. New York, NY: Cambridge University Press.

Hadfield, J. D., Wilson, A. J., Garant, D., Sheldon, B. C., & Kruuk, L. E. B. (2010). The misuse of BLUP in ecology and evolution. *The American Naturalist*, *175*, 116–125. https://doi.org/10.1086/648604

Hamilton, W. D. (1966). Moulding of senescence by natural selection. *Journal of Theoretical Biology*, *12*, 12–000.

Harvey, P. H., Greenwood, P. J., & Perrins, C. M. (1979). Breeding area fidelity of great tits (*Parus major*). *Journal of Animal Ecology*, *48*, 305–313. https://doi.org/10.2307/4115

Holtmann, B., Lagisz, M., & Nakagawa, S. (2017). Metabolic rates, and not hormone levels, are a likely mediator of between-individual differences in behaviour: A meta-analysis. *Functional Ecology*, *31*, 685–696. https://doi.org/10.1111/1365-2435.12779

Houle, D., Pelabon, C., Wagner, G. P., & Hansen, T. F. (2011). Measurement and meaning in biology. *Quarterly Review of Biology*, *86*, 3–34. https://doi.org/10.1086/658408

Houslay, T. M., & Wilson, A. J. (2017). Avoiding the misuse in BLUP in behavioral ecology. *Behavioral Ecology*, *28*, 948–952.

Hutfluss, A., & Dingemanse, N. J. (2019). Human recreation reduces clutch size in great tits Parus major regardless of risk-taking personality. *Behavioral Ecology*, *30*, 1751–1760.

Jenni, L., & Winkler, R. (1994). *Moult and ageing of European passerines*. London, UK: Academic Press.

Jones, O. R., Gaillard, J. M., Tuljapurkar, S., Alho, J. S., Armitage, K. B., Becker, P. H., … Coulson, T. (2008). Senescence rates are determined by ranking on the fast-slow life-history continuum. *Ecology Letters*, *11*, 664–673. https://doi.org/10.1111/j.1461-0248.2008.01187.x

Keller, L. F., Reid, J. M., & Arcese, P. (2008). Testing evolutionary models of senescence in a natural population: Age and inbreeding effects on fitness components in song sparrows. *Proceedings of the Royal Society B-Biological Sciences*, *275*, 597–604. https://doi.org/10.1098/rspb.2007.0961

Kluen, E., & Brommer, J. E. (2013). Context-specific repeatability of personality traits in a wild bird: A reaction-norm perspective. *Behavioral Ecology*, *24*, 650–658. https://doi.org/10.1093/beheco/ars221

Lemaitre, J. F., Berger, V., Bonenfant, C., Douhard, M., Gamelon, M., Plard, F., & Gaillard, J. M. (2015). Early-late life trade-offs and the evolution of ageing in the wild. *Proceedings of the Royal Society B: Biological Sciences*, *282*, 20150209. https://doi.org/10.1098/rspb.2015.0209

Mathot, K. J., & Frankenhuis, W. E. (2018). Models of pace-of-life syndromes (POLS): A systematic review. *Behavioral Ecology and Sociobiology*, *72*, 41. https://doi.org/10.1007/s00265-018-2459-9

Mathot, K. J., Nicolaus, M., Araya-Ajoy, Y. G., Dingemanse, N. J., & Kempenaers, B. (2015). Does metabolic rate predict risk-taking behaviour? A field experiment in a wild passerine bird. *Functional Ecology*, *29*, 239–249. https://doi.org/10.1111/1365-2435.12318

Medawar, P. B. (1952). *An unsolved problem in biology*. London, UK: H.K. Lewis & Co., Ltd..

Moiron, M., Araya-Ajoy, Y. G., Mathot, K. J., Mouchet, A., & Dingemanse, N. J. (2019). Functional relations between body mass and risk-taking behavior in wild great tits. *Behavioral Ecology*, *30*, 617–623. https://doi.org/10.1093/beheco/ary199

Montiglio, P. O., Dammhahn, M., Messier, G. D., & Reale, D. (2018). The pace-of-life syndrome revisited: The role of ecological conditions and natural history on the slow-fast continuum. *Behavioral Ecology and Sociobiology*, *72*, 9. https://doi.org/10.1007/s00265-018-2526-2

Nicolaus, M., Mathot, K. J., Araya-Ajoy, Y. G., Mutzel, A., Wijmenga, J. J., Kempenaers, B., & Dingemanse, N. J. (2015). Does coping style predict optimization: An experimental test in a wild passerine bird. *Proceedings of the Royal Society B-Biological Sciences*, *282*, 20142405. https://doi.org/10.1098/rspb.2014.2405

Nicolaus, M., Piault, R., Ubels, R., Tinbergen, J. M., & Dingemanse, N. J. (2016). The correlation between colouration and exploration behaviour varies across hierarchical levels in a wild passerine bird. *Journal of Evolutionary Biology*, *29*, 1780–1792.

Nicolaus, M., Tinbergen, J. M., Bouwman, K. M., Michler, S. P. M., Ubels, R., Both, C., … Dingemanse, N. J. (2012). Experimental evidence for adaptive personalities in a wild passerine bird. *Proceedings of the Royal Society B-Biological Sciences*, *279*, 4885–4892. https://doi.org/10.1098/rspb.2012.1936

Niemelä, P. T., & Dingemanse, N. J. (2018a). Meta-analysis reveals weak associations between intrinstic state and personality. *Proceedings of the Royal Society B-Biological Sciences*, *1873*, 20172823.

Niemelä, P. T., & Dingemanse, N. J. (2018b). On the usage of single measurements in behavioural ecology research on individual differences. *Animal Behavior*, *145*, 99–105. https://doi.org/10.1016/j.anbehav.2018.09.012

Niemelä, P., Dingemanse, N. J., Alioravainen, N., Vainikka, A., & Kortet, R. (2013). Personality pace-of-life hypothesis: Testing genetic associations among personality and life-history. *Behavioral Ecology*, *24*, 935–941. https://doi.org/10.1093/beheco/art014

Nussey, D. H., Kruuk, L. E. B., Donald, A., Fowlie, M., & Clutton-Brock, T. H. (2006). The rate of senescence in maternal performance increases with early-life fecundity in red deer. *Ecology Letters*, *9*, 1342–1350. https://doi.org/10.1111/j.1461-0248.2006.00989.x

Patrick, S. C., Charmantier, A., & Weimerskirch, H. (2013). Differences in boldness are repeatable and heritable in a long-lived marine predator. *Ecology and Evolution*, *3*, 4291–4299. https://doi.org/10.1002/ece3.748

Patrick, S. C., & Weimerskirch, H. (2015). Senescence rates and late adulthood reproductive success are strongly influenced by personality in a long-lived seabird. *Proceedings of the Royal Society B-Biological Sciences*, *282*, 20141649. https://doi.org/10.1098/rspb.2014.1649

Pauliny, A., Devlin, R. H., Johnsson, J. I., & Blomqvist, D. (2015). Rapid growth accelerates telomere attrition in a transgenic fish. *BMC Evolutionary Biology*, *15*, 159. https://doi.org/10.1186/s12862-015-0436-8

Réale, D., Garant, D., Humphries, M. M., Bergeron, P., Careau, V., & Montiglio, P. O. (2010). Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philosophical Transactions of the Royal Society of London Series B*, *365*, 4051–4063. https://doi.org/10.1098/rstb.2010.0208

Réale, D., Martin, J., Coltman, D. W., Poissant, J., & Festa-Bianchet, M. (2009). Male personality, life-history strategies and reproductive success in a promiscuous mammal. *Journal of Evolutionary Biology*, *22*, 1599–1607. https://doi.org/10.1111/j.1420-9101.2009.01781.x

Reid, J. M., Bignal, E. M., Bignal, S., McCracken, D. I., & Monaghan, P. (2003). Age-specific reproductive performance in red-billed choughs *Pyrrhocorax pyrrhocorax*: Patterns and processes in a natural population. *Journal of Animal Ecology*, *72*, 765–776. https://doi.org/10.1046/j.1365-2656.2003.00750.x

Ricklefs, R. E., & Wikelski, M. (2002). The physiology/life-history nexus. *Trends in Ecology and Evolution*, *17*, 462–468. https://doi.org/10.1016/S0169-5347(02)02578-8

Royaute, R., Berdal, M., Hickey, C., & Dochtermann, N. A. (2018). Paceless life? A meta-analysis of the "pace-of-life syndrome". *Behavioral Ecology and Sociobiology*, *72*, 64.

Saether, B. E. (1988). Pattern of covariation between life-history traits of European birds. *Nature*, *331*, 616–617. https://doi.org/10.1038/331616a0

Santostefano, F., Wilson, A. J., Niemelä, P. T., & Dingemanse, N. J. (2017). Behavioural mediators of genetic life-history trade-offs in field crickets: A test of the pace-of-life syndrome hypothesis in field crickets. *Proceedings of the Royal Society B: Biological Sciences*, *284*, 1864.

Smith, B. R., & Blumstein, D. T. (2008). Fitness consequences of personality: A meta-analysis. *Behavioral Ecology*, *19*, 448–455. https://doi.org/10.1093/beheco/arm144

Stamps, J. A. (2007). Growth-mortality tradeoffs and 'personality traits' in animals. *Ecology Letters*, *10*, 355–363. https://doi.org/10.1111/j.1461-0248.2007.01034.x

Stearns, S. C. (1992). *The evolution of life histories*. New York, NY: Oxford University Press.

Stuber, E. F., Araya-Ajoy, Y. G., Mathot, K. J., Mutzel, A., Nicolaus, M., Wijmenga, J. J., … Dingemanse, N. J. (2013). Slow explorers take less risk: A problem of sampling bias in ecological studies. *Behavioral Ecology*, *24*, 1092–1098. https://doi.org/10.1093/beheco/art035

Tarka, M., Guenther, A., Niemelä, P. T., Nakagawa, S., & Noble, D. W. A. (2018). Sex differences in life-history, behavior and physiology along a slow-fast continuum: A meta-analysis. *Behavioral Ecology and Sociobiology*, *72*, 132. https://doi.org/10.1007/s00265-018-2534-2

van de Pol, M., & Verhulst, S. (2006). Age-dependent traits: A new statistical model to separate within- and between-individual effects. *The American Naturalist*, *167*, 766–773. https://doi.org/10.1086/503331

van Noordwijk, A. J., McCleery, R. H., & Perrins, C. M. (1995). Selection for the timing of great tit breeding in relation to caterpillar growth and temperature. *Journal of Animal Ecology*, *64*, 451–458. https://doi.org/10.2307/5648

Verbeek, M. E. M., Drent, P. J., & Wiepkema, P. R. (1994). Consistent individual differences in early exploratory behaviour of male great tits. *Animal Behaviour*, *48*, 1113–1121. https://doi.org/10.1006/anbe.1994.1344

Williams, G. C. (1957). Pleiotropy, natural selection, and the evolution of senescence. *Evolution*, *11*, 398–411. https://doi.org/10.1111/j.1558-5646.1957.tb02911.x

Williams, G. C. (1966). Natural selection costs of reproduction and a refinement of Lack's principle. *The American Naturalist*, *100*, 687–690.

Wolf, M., van Doorn, G. S., Leimar, O., & Weissing, F. J. (2007). Life-history trade-offs favour the evolution of animal personalities. *Nature*, *447*, 581–585. https://doi.org/10.1038/nature05835

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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